Main prey and predators of capelin (*Mallotus villosus*) in the northern and southern Gulf of St. Lawrence during the mid-1980s and mid-1990s

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ABSTRACT

Savenkoff, C., F. Grégoire, and D. Chabot. 2004. Main prey and predators of capelin (*Mallotus villosus*) in the northern and southern Gulf of St. Lawrence during the mid-1980s and mid-1990s. Can. Tech. Rep. Fish. Aquat. Sci. 2551: vi+30 pp.

Based on the results of mass-balance models, we present here the changes in the structure and functioning of the northern and southern Gulf of St. Lawrence ecosystems related to the capelin stock (*Mallotus villosus*) from the pre- to post-collapse period of the groundfish stocks, which were the main predators of capelin. The net decrease in biomass of these demersal species and the ensuing drop in predation from the mid-1980s to the mid-1990s led to an ecosystem structure dominated by small-bodied pelagic species and marine mammals in the northern and southern Gulf. Capelin is an important prey for many fish species (cod [*Gadus morhua*] and redfish [*Sebastes* spp.] in the northern Gulf; cod and mackerel [*Scomber scombrus*] in the southern Gulf) and for marine mammals (cetacea and seals). Capelin plays a key role in the food web by transferring energy from primary and secondary producers (on which it feeds) to higher trophic levels of the demersal and pelagic domains of the Gulf of St. Lawrence. Capelin was the main fish predator of small and large zooplankton in the northern Gulf for each time period and was also the main prey consumed by fish and marine mammals.

RÉSUMÉ

Savenkoff, C., F. Grégoire et D. Chabot. 2004. Main prey and predators of capelin (*Mallotus villosus*) in the northern and southern Gulf of St. Lawrence during the mid-1980s and mid-1990s. Can. Tech. Rep. Fish. Aquat. Sci. 2551: vi+30 pp.

Basé sur les résultats de modèles d'équilibre de masse, nous présentons ici les changements dans la structure et le fonctionnement des écosystèmes du nord et du sud du golfe du Saint-Laurent associés au stock de capelan (*Mallotus villosus*) avant et après l'effondrement des stocks de poissons de fond qui étaient les principaux prédateurs du capelan. La forte diminution des biomasses de ces espèces démersales et la chute résultante de leur prédation depuis le milieu des années 1980 au milieu des années 1990 ont conduit à une structure de l'écosystème dominée par des petits poissons pélagiques et des mammifères marins dans le nord et le sud du golfe du Saint-Laurent. Le capelan est une importante proie pour de nombreuses espèces de poissons (morue [*Gadus morhua*] et sébaste [*Sebastes* spp.] dans le nord du Golfe ; morue et maquereau [*Scomber scombrus*] dans le sud du Golfe) et pour les mammifères marins (cétacés et phoques). Le capelan joue un rôle clé dans le réseau trophique en transférant l'énergie depuis les producteurs primaires et secondaires aux niveaux trophiques supérieurs des domaines démersal et pélagique du golfe du Saint-Laurent. Le capelan était le principal poisson prédateur du petit et grand zooplancton dans le nord du Golfe à chaque période de temps tout en étant la principale proie consommée par les poissons et les mammifères marins.

PREFACE

From 1992 to 1994, moratoria on fishing for Atlantic cod (*Gadus morhua*) were declared after Canadian east coast stocks collapsed, thus ending one of the largest and longest running commercial groundfish fisheries in the world. More than a decade later, in spite of limited fishing, almost all of these stocks show no signs of recovery. The reasons for the failure of these stocks to recover are not well understood. Consequently, the Department of Fisheries and Oceans developed a multi-year research program entitled "Comparative Dynamics of Exploited Ecosystems of the Northwest Atlantic" (CDEENA) to examine changes that might have occurred in the northwest Atlantic ecosystems over the last 15 years. The objective was to develop individual ecosystem models for the northern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization [NAFO] divisions 4RS), the southern Gulf of St. Lawrence (NAFO division 4T), the Newfoundland and Labrador coast and offshore region (NAFO divisions 2J3KLNO), and the Scotian Shelf region off the coast of Nova Scotia (NAFO divisions 4VsWX) prior to the groundfish collapses of the early 1990s in virtually all areas (mid-1980s) and after this period (mid-1990s), when the collapsed groundfish stocks had failed to recover.

INTRODUCTION

In the early 1990s, the abundance of many northwest Atlantic cod (*Gadus morhua*) populations declined to low levels resulting in the cessation of directed fishing for these stocks, thus ending one of the largest and longest running commercial groundfish fisheries in the world (CAFSAC 1994). Ten years later, few stocks show signs of recovery (DFO 2003). The reasons for the failure of these stocks to recover are not well understood.

Mass-balance models using inverse methodology have been constructed for the northern Gulf of St. Lawrence ecosystem (Savenkoff et al. in press; Savenkoff et al. submitted a[1]) and for the southern Gulf of St. Lawrence ecosystem (Savenkoff et al. submitted b[2]) before (mid-1980s) and after (mid-1990s) the collapse of groundfish stocks, in an attempt to understand the ecosystem changes that may explain the failure of these stocks to recover in the 1990s.

Savenkoff et al. (submitted b) showed that the southern ecosystem structure shifted dramatically from one dominated by piscivorous groundfish and small-bodied forage species (e.g., capelin [*Mallotus villosus*], herring [*Clupea harengus harengus*], and shrimp [mainly *Argis dentata*, *Eualus macilentus*, and *E. gaimardi*]) in similar proportions during the mid-1980s to one dominated by small-bodied forage species and marine mammals during the mid-1990s. Predation by marine mammals on fish increased slightly from the pre- to post-collapse period (from 2.33 ± 0.31 to 2.79 ± 0.39 t km^{-2} yr^{-1}; i.e., from 27 to 38%) while predation by fish on fish decreased (from 3.93 ± 0.32 to 2.95 ± 0.64 t km^{-2} yr^{-1}; i.e., from 45 to 40%). A similar change in the ecosystem structure of the northern Gulf was observed (Savenkoff et al. submitted a). There, predation by marine mammals increased from 21 to 53% of total mortality while predation by fish decreased from 49 to 28%. Due to the drastic decline in the biomass of large cod (from 3.93 to 0.27 t km^{-2}), seals replaced large cod as the main predators in the northern Gulf during the mid-1990s (Savenkoff et al. submitted a). In contrast, while the effects of seals also increased during the mid-1990s, large cod remained the most important single predator on fish in the southern Gulf, though the combined predation by harp (*Phoca groenlandica*) and grey (*Halichoerus grypus*) seals did exceed predation by large cod (Savenkoff et al. submitted b).

These changes were accompanied by a decrease in total catches of about 30% (from 2.80 ± 0.15 to 2.01 ± 0.08 t km^{-2} yr^{-1}) and a transition in catches from long-lived piscivorous groundfish toward planktivorous pelagic fish in the southern Gulf (Savenkoff et al. submitted b). A similar trend was observed in the northern Gulf over the same period of time (Savenkoff et al. submitted a). However, total catches in the northern Gulf decreased much more (by a factor of 4) from the mid-1980s (1.83 ± 0.07 t km^{-2} yr^{-1}) to mid-1990s (0.47 ± 0.04 t km^{-2} yr^{-1}). Reported cod catches accounted for 51% of the total fishery in the northern Gulf during the mid-1980s while forage fish and invertebrates represented only 26% of total catches. The fishery in the southern Gulf was more diverse during the mid-1980s, with only 39% of total catches represented by cod while forage fish and invertebrates represented 52% of total catches. Thus, the decline in total catches when cod stocks collapsed was lower in the southern Gulf than in the northern Gulf.

There is a general agreement that the primary reason for the groundfish collapse was overfishing (e.g., Hutchings and Myers 1994; Hutchings 1996; Myers et al. 1996). Results from ecosystem modelling suggest that overfishing during the mid-1980s also caused major changes in the structure and functioning of the Gulf ecosystems over the last two decades. Here we present the changes in the structure and functioning of the Gulf ecosystems from the pre- to post-collapse period of the groundfish stocks as they relate to capelin stocks (*Mallotus villosus*).

[1]: Savenkoff, C., Castonguay, M., Bourdages, H., Chabot, D., Morissette, L., and Hammill, M. O. Effects of fishing and predation in a heavily exploited ecosystem I: Comparing pre- and post-groundfish collapse periods in the northern Gulf of St. Lawrence (Canada). Submitted to Can. J. Fish. Aquat. Sci.

MATERIAL AND METHODS

Data used in modelling

The data set covers a region (depths > 37 m) of the northern Gulf of St. Lawrence (Northwest Atlantic Fishing Organization [NAFO] divisions 4RS) equivalent to a total area of 103,812 km^2 (Figure 1). The sampling region used in our models for the calculation of densities was the surface of strata sampled for the summer research survey in the northern Gulf of St. Lawrence. In the southern Gulf (NAFO division 4T), the study covers a 64,075 km^2 area between the depths of 15 and 200 m (Figure 1). Infra-littoral species and American lobster (*Homarus americanus*) were not included in the models. This zone was excluded from the models because exchanges between the infra-littoral and pelagic zones are still poorly understood. The periods covered by this analysis are the pre-collapse (mid-1980s: 1985–1987) and post-collapse (mid-1990s: 1994–1996) periods of groundfish stocks in most areas of the Northwest Atlantic.

Based on data availability and the ecological and commercial significance of the species, the whole-system model was divided into 32 functional groups or compartments in the northern Gulf and 30 functional groups in the southern Gulf, representing the main pelagic, demersal, and benthic species present (Table 1), which are interconnected by mass flows of matter. We distinguished five marine mammal groups, one seabird group, fourteen (in the southern Gulf) or sixteen (in the northern Gulf) fish groups, eight invertebrate groups, one phytoplankton group, and one detritus group (Table 1). Some groups, such as large pelagic and demersal feeders, are composite groups, where the species were aggregated based on similarity in size and ecological role. Cod, Greenland halibut (*Reinhardtius hippoglossoides*) (in the northern Gulf), and American plaice (*Hippoglossoides platessoides*) (in the southern Gulf) were, for some models, separated into two groups based on diet, age/size at first capture, and age/size at maturity. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but for these models it was assumed that the change occurs at 35 cm for cod (Lilly 1991) and American plaice (Pitt 1973), and at 40 cm for Greenland halibut (Bowering and Lilly 1992). Due to a lack of data, we could not distinguish juveniles and adults for other fish species. Finally, bacteria were considered part of the detritus compartment (Table 1).

To estimate the magnitude of the trophic fluxes, the models require measurements or estimates of different parameters (input data) such as biomass, diet composition, and landings as well as consumption and production rates for different living compartments. Diet composition and the other input data (biomass, production, consumption, catch) for each compartment can be found in Morissette et al. (2003) and Savenkoff et al. (2004 a, b).

[2]: Savenkoff, C., Swain, D. P., Hanson, J. M., Castonguay, M., Hammill, M. O., Bourdages, H., Morissette, L., and Chabot, D. Effects of fishing and predation in a heavily exploited ecosystem II: Comparing pre- and post-groundfish collapse periods in the southern Gulf of St. Lawrence (Canada). Submitted to Can. J. Fish. Aquat. Sci.

Inverse modelling

Inverse models are mass-balance models. These models generate a "snapshot" of the system at one moment in time and use mass-balance principles and an objective least-squares criterion to estimate flows of organic matter or energy among components of an ecosystem (Vézina and Platt 1988; Savenkoff et al. in press). These models, as opposed to traditional approaches, consider the ecosystem as a whole rather than its components separately and provide a description of trophic interactions between all functional groups of the modelled ecosystem. Inverse methods provide a powerful tool to estimate ecosystem flows using limited data and straightforward mass balance and metabolic constraints. Simulated inverse analyses have shown that the general flow structure of ecosystems can be recovered with these techniques, although the details can be inaccurate (Vézina and Pahlow 2003). The inverse methodology is also able to generate alternative scenarios (or solutions) that explain the data.

Under the steady–state assumption, consumption representing the input must balance the sum of the outputs consisting of production, respiration, and egestion (flux of unassimilated food: feces or detrital flow) for each group. In these models, we assumed that there was no year-to-year change in biomass during each of the two studied time periods and that net migration was zero (migration out of or into the study area, food intake by predators that are not part of the system, etc.). Thus, production was simply the biomass lost to predation, natural mortality other than predation (disease, other natural causes of death, and unexplained mortality [unsuspected processes occurring in the ecosystem]; hereafter termed other mortality), and fishing mortality. For phytoplankton, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus were assumed to respire. Details of the model structure and method of solution for the different equations are given in Savenkoff et al. (in press and submitted a, b).

The use of upper and lower limits to constrain the majority of input values (production, consumption, catch, and diet composition) and the choice of row and column weights make inverse modelling a flexible tool to quantify mass-balanced flow diagrams and trophic transfer efficiencies that are internally consistent. However, mass-balance models estimated a very large number of parameters, and it is possible that the relatively limited data available were insufficient to constrain these parameters. Also, where one modelling approach compromises or simplifies portions of the system, another may provide a realistic and precise representation of the same parts of the system (Whipple et al. 2000). By randomly perturbing the data inputs within their uncertainty range, Savenkoff et al. (in press and submitted a, b) constructed a set of balanced solutions, and the final solution of inverse modelling was the mean of at least 31 balanced random perturbations (including a response without perturbation) for each model and each time period. The estimated flows fell inside our a priori constraints (once the data were perturbed) and therefore are a reasonable "middle ground" description (Savenkoff et al. submitted a, b). The models were useful in constraining observations into coherent pictures. However, since the number of flows to be solved exceeds the number of independent mass balance relations (i.e., an underdetermined system), other equivalent solutions remain possible.

Capelin background

Capelin is a small, short-lived pelagic fish that spends most of its life offshore, moving inshore only to spawn. The species is exploited commercially in some areas and is probably the most important forage fish of the Gulf of St. Lawrence (DFO 2001).

The capelin fishery in the Estuary and Gulf of St. Lawrence developed rapidly with the emergence of a Japanese market for the roe-bearing females in the late 1970s (DFO 2001). Annual landings have risen to nearly 10,000 t from a level of 700 t at that time (Figure 2). The bulk of the catches are made by purse seiners on the west coast of Newfoundland. In addition to recreational fishery landings made during beach spawning, capelin is a by-catch of shrimp (*Pandalus borealis*) harvesting. Although the structure of the species' population is relatively unknown, capelin are managed as two separate management units, i.e., NAFO divisions 4ST and 4R, whose total allowable catches (TACs) in 2002 were 1,725 t and 10,700 t, respectively.

Input data (biomass, production, consumption, and catch) used in the modelling and estimated fluxes for capelin for each ecosystem and each period are summarized in Table 2.

Catch

Commercial landings were estimated from NAFO landing statistics (NAFO 1999). In the northern Gulf, the mean annual total catch was 2,408 t or 2.32×10^{-2} t km^{-2} yr^{-1} (SD = 1.37×10^{-2} t km^{-2} yr^{-1}) during the 1985–1987 period and 2,536 t or 2.45×10^{-2} t km^{-2} yr^{-1} (SD = 4.97×10^{-2} t km^{-2} yr^{-1}) during the 1994–1996 period. In the southern Gulf, the mean annual catch of capelin was 185 and 127 t during the 1985–1987 and 1994–1996 periods, respectively (NAFO 1999). Since the study area covered only a fraction of 4T (area between the depths of 15 and 200 m), a correction factor for catch was used. This correction factor, estimated using the biomass ratio between the study area and 4T, was 0.92 and 0.96, respectively, for the two periods. This resulted in a mean annual catch of capelin of 2.89×10^{-3} t km^{-2} yr^{-1} (SD = 4.12×10^{-3} t km^{-2} yr^{-1}) during the 1985–1987 period and 1.91×10^{-3} t km^{-2} yr^{-1} (SD = 1.07×10^{-3} t km^{-2} yr^{-1}) during the 1994–1996 period.

Biomass

In the northern Gulf, annual biomass estimates of capelin were obtained from the *Lady Hammond* scientific surveys for the 1985–1987 period and from the *Needler* scientific surveys for the 1994–1996 period using the *PACES* software (DFO, groundfish survey database, unpublished data). Trawlable biomass estimates were converted to catchability-adjusted biomass based on catchability coefficients estimated by Harley and Myers (2001) and Savenkoff et al. (2004). For the 1985–1987 period, this resulted in a mean annual biomass estimate of 3,454,554 t or 33.28 t km^{-2}. Since the biomass of this group was a gross approximation (the catchability for capelin is not very good with the fishing gear used by the groundfish survey), we also used an estimate (0.07 t km^{-2}) for the Lower St. Lawrence Estuary from acoustic surveys (Y. Simard, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, personal communication). This resulted in a mean

biomass of 16.67 ± 23.48 t km^{-2} (range: 0.07–33.28 t km^{-2}) during the mid-1980s. For the 1994–1996 period, a mean annual biomass of 45,320,090 t or 436.56 t km^{-2} (range: 173.67–802.78 t km^{-2}) was obtained. This range seemed unrealistic and thus we decided to use the acoustic estimate as lower limit. The biomass range used for the mid-1990s was 0.07 to 802.78 t km^{-2}. However, we used the mean biomass (16.67 t km^{-2}) determined for the mid-1980s to calculate the production/biomass and consumption/biomass ratios for the two periods in the northern Gulf.

In the southern Gulf, annual biomass estimates were obtained from the groundfish survey that is conducted each September. The length–frequency data were corrected for catchability. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean weight-at-length (derived from length–weight relationships) and summing the results. The mean biomass estimate for capelin was 8,044 t or 0.13 ± 0.18 t km^{-2} (range: 0.00–0.33 t km^{-2}) and 1,379,380 t or 21.53 ± 23.79 t km^{-2} (range: 5.11–48.81 t km^{-2}) during the mid-1980s and mid-1990s, respectively. However, during the mid-1980s, based on initial inverse modelling runs, the previous value for capelin seemed to be too low to meet predator demands (0.98 t km^{-2}) (Savenkoff et al. 2004b). We used a biomass range of 0.00 to 0.98 t km^{-2}, corresponding to a mean biomass of 0.49 ± 0.69 t km^{-2} during the mid-1980s. The biomass estimate for the mid-1990s was a gross approximation and seemed to be too high. In fact, based on the final inverse model, the required biomass to meet predator demands was 5.60 t km^{-2} during the mid-1990s (Savenkoff et al. 2004b).

Production

Due to the lack of reliable information on production (P) and total mortality (Z) for capelin in NAFO divisions 4RST, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch (Allen 1971). Natural mortality was set to 0.6 yr^{-1} to reflect the biology of this short-lived species.

In the northern Gulf, when the minimum and maximum biomass values were used for each period, we obtained production ranges of 0.04 to 19.99 t km^{-2} yr^{-1} (mean: 10.02 ± 14.10 t km^{-2} yr^{-1}) and 0.08 to 481.70 t km^{-2} yr^{-1} (mean: 10.04 ± 14.19 t km^{-2} yr^{-1}) during the mid-1980s and mid-1990s, respectively. The modelling production estimate for capelin was 13.56 t km^{-2} yr^{-1} and 3.07 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively.

In the southern Gulf, we obtained a production range of 0.001 to 0.21 t km^{-2} yr^{-1}, when the minimum and maximum biomass values were used for the mid-1980s. However, based on initial inverse modelling runs, these values seemed to be too low to meet predator demands. A production of 0.61 t km^{-2} yr^{-1} was required and was thus used as the maximum production limit. This maximum production value was related to a biomass value of 0.98 t km^{-2} (see previous biomass section). The resulting lower and upper production limits were thus 0.001 to 0.61 t km^{-2} yr^{-1} (mean: 0.30 ± 0.43 t km^{-2} yr^{-1}) during the mid-1980s. The modelling production estimate for capelin was 0.55 t km^{-2} yr^{-1} during the mid-1980s.

When the initial minimum and maximum biomass values were used for the mid-1990s in the southern Gulf, we obtained a production range of 2.31 to 29.29 t km^{-2} yr^{-1} (mean: 11.32 ± 17.86 t km^{-2} yr^{-1}). The modelling production estimate for capelin was 2.94 t km^{-2} yr^{-1} during the mid-1990s. Thus, based on the initial P/B ratio of 0.53 yr^{-1}, the biomass required to meet predator demands was 5.60 t km^{-2} during the mid-1990s (see previous biomass section).

Consumption

Consumption rate for capelin was taken from various sources. A Q/B ratio (3.80 yr^{-1}) was determined using FishBase for a water temperature of 1°C, considering that this species is generally found near the cold intermediate layer in the Gulf of St. Lawrence (Froese and Pauly 2002). We used a second estimate based on the feeding ecology of capelin in the Estuary and western Gulf of St. Lawrence (Vesin et al. 1981). The daily ration was estimated at 5.00% of body mass in summer and 2.50% of body mass in winter, giving a mean of 3.75% of body mass per day. From these values, the mean annual Q/B ratio was estimated to be 13.69 yr^{-1}. A third Q/B estimate was determined from a summer study on Barents Sea capelin (Ajiad and Pushaeva 1991). Daily ration was estimated to be between 1.47% and 2.00% of the body mass, resulting in an average Q/B ratio of 6.33 yr^{-1}. Finally, Panasenko (1981) estimated a Q/B ratio of 27.56 yr^{-1} in another study in the Barents Sea.

In the northern Gulf, the model for the mid-1980s was completed without including the study of Panasenko (1981). We used the minimum and maximum biomass values and the three previous Q/B ratios to obtain a consumption range of 0.56 to 264.22 t km^{-2} yr^{-1}. Consumption values were also estimated assuming a gross growth efficiency (GE; the ratio of production to consumption) ranging between 10 and 30% (Christensen and Pauly 1992). The consumption values based on the mean production (10.02 t km^{-2} yr^{-1}) and the minimum and maximum GE limits (10–30%) were 33.39 to 100.16 t km^{-2} yr^{-1}. The resulting range used was 0.56 to 264.22 t km^{-2} yr^{-1}. The consumption value estimated by the inverse solution was 58.06 t km^{-2} yr^{-1} (Q/B = 3.48 yr^{-1}) for capelin during the mid-1980s. During the mid-1990s, we obtained a consumption range of 0.27 to 22,122.51 t km^{-2} yr^{-1} when the resulting minimum and maximum biomass values were used for the mid-1980s and based on the four previous Q/B ratios. Based on the previous mean production (10.04 t km^{-2} yr^{-1}) for capelin and the minimum and maximum GE limits (10–30%), we obtained other consumption values of 33.46 and 100.38 t km^{-2} yr^{-1}. We decided to use 0.27–100.38 t km^{-2} yr^{-1} as the lower and upper limit constraints. The consumption value estimated by the inverse solution was 15.49 t km^{-2} yr^{-1} (Q/B = 0.93 yr^{-1}) for capelin during the mid-1990s.

In the southern Gulf, when using the resulting minimum and maximum biomass values for the mid-1980s and based on the four previous Q/B ratios, we obtained a consumption range of 0.00 to 26.88 t km^{-2} yr^{-1}. During the mid-1990s, when the initial minimum and maximum biomass values were used, we obtained a consumption range of 19.41 to 1,344.99 t km^{-2} yr^{-1}. Based on the mean production (0.30 and 11.32 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 1.02 to 3.04 and 37.72 to 113.17 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively. Assuming that this species would eat at least as much food as its biomass (Q/B $\geq$ 1), the resulting lower and upper consumption limits were thus 0.49 (instead of 0.00) to 26.88 t km^{-2} yr^{-1} and 21.53 (instead of 19.41) to 1,344.99 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 2.67 t km^{-2} yr^{-1} (Q/B = 5.47 yr^{-1}) and 22.62 t km^{-2} yr^{-1} (Q/B = 1.05 yr^{-1} or 4.04 yr^{-1} if we used the estimated biomass of 5.60 t km^{-2}) for capelin during the mid-1980s and mid-1990s, respectively.

Diet composition

In the northern Gulf, the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Jangaard (1974) for the North Atlantic were used. Main prey items were copepods (*Temora longicornis*, *Calanus finmarchicus*, and *Pseudocalanus minutus*) and euphausiid eggs. We also used the study of Vesin et al. (1981) in the Estuary and western Gulf of St. Lawrence. In that study, euphausiids and copepods were the main prey (59 and 41%, respectively). The final diet compositions used for the two periods are shown in Table 3.

In the southern Gulf, we used only the diet composition estimated by Vésin et al. (1981) in the Estuary and western Gulf of St. Lawrence from 1974 to 1975. In that study, euphausiids and copepods were the main prey (6.3 and 93.7%, respectively) (Table 4).

RESULTS

Main prey groups consumed by capelin

Large zooplankton (mainly the euphausiids *Thysanoessa rashii* and *Meganyctiphanes norvegica*) and small zooplankton (mainly the calanoid copepod *Calanus finmarchicus*) were the main prey during the two periods in the northern Gulf (Figure 3). Small and large zooplankton accounted for 59 and 36%, respectively, of the diet during the mid-1980s while they each contributed 49% of the diet during the mid-1990s. This similarity in diet is due to a lack of knowledge on the local diet for each period, which resulted in the same diet being input in both models. Since the mean size of capelin has declined between the two periods (Grégoire et al. 1999; MPO 1999; Carscadden and Frank 2002), and since feeding on small zooplankton (copepods) versus macrozooplankton changes with capelin size (Gerasimova 1994; O'Driscoll et al. 2001; Gjøsæter et al. 2002), future versions of these models could relate the ratio of small to large zooplankton to average capelin size. A decrease in the capelin consumption was estimated by the models from the mid-1980s to the mid-1990s (from 58.1 ± 10.4 to 15.5 ± 8.6 t km^{-2} yr^{-1}; Figure 3). In fact, this result reflects the decrease in the capelin biomass required to meet predator demands in relation to the decline in abundance and the predatory role of piscivorous fish between the two periods modelled. This result may be an artefact of the model due to the lack of information on capelin.

In the southern Gulf, small zooplankton (mainly the cyclopoid copepod *Oithona similis*) were the most important prey for the two periods (nearly 93% of the diet for each time period) while large zooplankton (e.g., chaetognaths, jellies) accounted only for only about 7% of the diet for each time period (Figure 4). Again, this reflects the fact that the same diet was input in both models due to lack of local knowledge on capelin diet; an adjustment for average capelin size in future models is desirable. An increase in capelin consumption was estimated by the models from the mid-1980s to the mid-1990s (from 2.7 ± 1.7 to 22.6 ± 3.7 t km^{-2} yr^{-1}; Figure 4) in relation to the increase in capelin biomass.

Role played by capelin in the northern and southern Gulf ecosystems

In the northern Gulf, there was a four-fold decrease in the matter consumed from the pre- to post-collapse period (Figure 5). When planktonic prey were not considered in the calculation, capelin was the major prey in the system and accounted for 56 and 58% of all matter consumed in the mid-1980s and the mid-1990s, respectively (Figure 5). The three other main prey groups were sand lance (*Ammodytes* spp.), redfish, and shrimp (mostly *Pandalus borealis*) during the mid-1980s. During the mid-1990s, shrimp, redfish, and planktivorous small pelagics (mainly Atlantic herring *Clupea harengus*) were heavily consumed in the ecosystem.

In the southern Gulf, there was no difference in the amount of matter consumed within the ecosystem from the pre- to post-collapse period (8.1 t km^{-2} yr^{-1}; Figure 6). However, the relative size of the compartments processing this matter changed substantially. When planktonic prey were not considered, planktivorous small pelagics, shrimp, small American plaice, and piscivorous small pelagics (mainly Atlantic mackerel *Scomber scombrus*) were the main prey in the southern Gulf (combined = 64% of all matter consumed) during the mid-1980s (Figure 6). In contrast, capelin was the most important prey during the 1990s followed by shrimp, planktivorous small pelagics, and small American plaice (combined = 78% of all matter consumed).

Main causes of capelin mortality

In the northern Gulf, predation was the main cause of total capelin mortality during the mid-1980s (79.9% of total mortality; Figure 7). Natural mortality other than predation and fishing mortality represented 19.9 and 0.2% of total mortality. Large cod was the main predator followed by redfish. Also, capelin cannibalism accounted for 7%. From the pre- to post-collapse period, there was a four-fold decrease in total mortality (from 13.6 ± 3.4 to 3.1 ± 0.7 t km^{-2} yr^{-1}; Figure 7). Predation mortality decreased from 10.8 ± 2.9 t km^{-2} yr^{-1} during the mid-1980s to 2.7 ± 0.6 t km^{-2} yr^{-1} during the mid-1990s. Predation dominated total mortality (88.1% of total mortality) during the mid-1990s while natural mortality other than predation and fishing accounted for 10.8 and 1.1%, respectively. Cetacea and harp seals were the main predators of capelin; however, their predation fluxes were lower than those of large cod and redfish during the mid-1980s (Figure 7).

In the southern Gulf, predation was also the main cause of total capelin mortality during the mid-1980s (94.3% of total mortality; Figure 8). Natural mortality other than predation and fishing mortality represented 5.1 and 0.5% of total mortality. Harp seals were the main predators followed by large cod and seabirds. From the pre- to post-collapse period, there was a five-fold increase in total mortality (Figure 8). Predation mortality increased from 0.5 ± 0.1 t km^{-2} yr^{-1} during the mid-1980s to 2.9 ± 0.6 t km^{-2} yr^{-1} during the mid-1990s. Predation dominated total mortality (73.0% of total mortality) during the mid-1990s while natural mortality other than predation and fishing accounted to 27.0 and 0.1%, respectively. Harp seals were the main predators followed by piscivorous small pelagics and large cod (Figure 8).

Trophic links related to capelin

In the northern Gulf of St. Lawrence for the two periods, predation was the dominant cause of fish mortality (on average 70 and 83% of total mortality during the mid-1980s and the mid-1990s, respectively). The high level of predation was supported by a large pelagic forage base, which included capelin, sand lance, and small pelagic feeders. When planktonic prey were not considered, capelin was the major prey in the system for each period. Capelin was mainly preyed upon by large cod and redfish during the mid-1980s while whales and harp seals exerted the main predation pressure during the mid-1990s (Figure 9). Capelin was the main predator of large zooplankton, and it had a non-negligible predation impact (main fish predator) on the small zooplankton for each period (Figure 9). Small and large zooplankton were the major consumers of phytoplankton: they were responsible for 82 and 11% of the phytoplankton grazing during the mid-1980s and 82 and 8% of the phytoplankton grazing during the mid-1990s. Also, when small zooplankton cannibalism was not considered, large zooplankton exerted the largest predation pressure on small zooplankton. Capelin was thus the critical converter of energy produced at lower trophic levels (phytoplankton–zooplankton) to a form available to other fish, marine mammals, and sea birds in the northern Gulf. Capelin was the main fish predator of small and large zooplankton in the northern Gulf for each time period and was also the main prey consumed by fish and marine mammals.

In the southern Gulf, the pattern was relatively similar (Figure 10). The role played by capelin in the ecosystem increased during the mid-1990s in relation to a rise in capelin biomass during the mid-1990s. In fact, this increase in biomass offset the decreases in the biomasses of both piscivorous small pelagics (mainly Atlantic mackerel) and planktivorous small pelagics (mainly Atlantic herring) during the mid-1990s. The biomass of forage fish (capelin and small pelagic feeders) thus changed little during the two periods. During the mid-1980s, piscivorous small pelagics and planktivorous small pelagics were the main predators of large zooplankton and they had a non-negligible predation impact (main fish predators) on the small zooplankton for each period. During the mid-1990s, planktivorous small pelagics were the main fish predators of large zooplankton. Capelin was the main fish predator of small zooplankton and highly consumed large zooplankton (nearly an eight-fold increase each in the predation by capelin on small and large zooplankton; Figure 10). Small pelagic feeders and capelin were also the main prey consumed by fish and marine mammals in the southern Gulf and were thus the major players in the transfer of organic matter from its entry into the system (by primary or phytoplankton production and zooplankton) to the upper trophic level of the demersal and pelagic domains in the southern Gulf.

DISCUSSION / CONCLUSION

The abundance of many northwest Atlantic groundfish populations declined to low levels in the early 1990s, resulting in moratoria on directed fishing for these stocks (CAFSAC 1994). In the Gulf of St. Lawrence, dramatic declines in the biomass of the large-bodied demersal predators such as Atlantic cod (fifteen-fold in the northern Gulf and three-fold in the southern Gulf), redfish (eight-fold in the northern Gulf), large American plaice (two-fold in the southern Gulf), and large demersals (four-fold in the northern Gulf and three-fold in the southern Gulf)

occurred from the pre- (mid-1980s) to post- (mid-1990s) collapse periods. In fact, only the biomass of marine mammals increased significantly (nearly two-fold). These changes were accompanied by a decrease in total catches and a transition in landings from long-lived and piscivorous groundfish toward planktivorous pelagic fish and invertebrates (Savenkoff et al. submitted a, b).

Predation by seals increased significantly from the mid-1980s to the mid-1990s while predation by fish decreased in the two ecosystems (Savenkoff et al. in press and submitted a, b). The net decrease in biomass of the demersal species and the ensuing drop in predation from the mid-1980s to the mid-1990s led to an ecosystem structure dominated by small-bodied pelagic species and marine mammals in the northern and southern Gulf.

Capelin plays a key role in the food web by transferring energy from primary and secondary producers (on which it feeds) to higher trophic levels. It is an important prey for many fish species (cod and redfish in the northern Gulf, cod and mackerel in the southern Gulf) and for marine mammals (cetacea and seals) (Piatt and Methven 1992; Lawson et al. 1998; DFO 2001; this study). Our estimates show that predators annually consumed 1.1×10^6 t or 10.8 t km^{-2} yr^{-1} of capelin in the northern Gulf during the mid-1980s and 2.8×10^5 t or 2.7 t km^{-2} yr^{-1} during the mid-1990s. In the southern Gulf, the predator demands increased four-fold, from 3.3×10^4 t or 0.5 t km^{-2} yr^{-1} during the mid-1980s to 1.4×10^5 t or 2.1 t km^{-2} yr^{-1} during the mid-1990s. In fact, in the two ecosystems, we observed a switch in the proportion of main prey in the diets of seals (mainly harp and grey seals) from the mid-1980s to the mid-1990s. Indeed, in the mid-1980s, small cod was important in the harp seal and grey seal diets while it was replaced by a higher proportion of capelin in the mid-1990s (Savenkoff et al. 2004a, b). This switch is consistent with observed changes in the relative abundance of the two prey species (decrease in cod biomass and increase or equality in capelin biomass) from the mid-1980s to the mid-1990s in the northern and southern Gulf. Capelin is a regular catch in the annual groundfish research surveys conducted in the northern and southern Gulf of St. Lawrence. Since the 1990, capelin catches have clearly shown a significant expansion in its geographical distribution in the entire Gulf of St. Lawrence (DFO 2001). This expansion is confirmed by an increase of the contribution of capelin to the diet compositions of cod (small cod: from 0.0 to 2.1%; large cod: from 2.0 to 5.5%) and mackerel (from 6.7 to 11.4%) from the mid-1980s to the mid-1990s in the southern Gulf (Savenkoff et al. 2004b).

The input data for capelin production, consumption, and diet composition were obtained from other areas and/or time periods (Morissette et al. 2003; Savenkoff et al. 2004 a, b), resulting in considerable uncertainty in these parameters. Also, the biomass of this group was a gross approximation (the catchability of capelin is not very good with the fishing gear used by the groundfish survey) for each ecosystem and each period. Initially, the mean annual biomass was 436.56 t km^{-2} during the mid-1990s in the northern Gulf; however, this value seemed too high. Thus, capelin biomass was assumed to be the same in both periods in the northern Gulf. With the decrease in predation mortality from the mid-1980s to the mid-1990s in the northern Gulf, an increase in capelin biomass would be expected. However, in contrast to the pattern in the southern Gulf, the modelling results did not show this trend and rather a decrease in the capelin consumption was estimated (e.g., the trophic fluxes from small and large zooplankton decreased from the mid-1980s to the mid-1990s; Figure 9). In fact, this result reflects the decrease in the capelin biomass required to meet predator demands (Table 2) in relation to the decline in abundance and the predatory role of piscivorous fish between the two periods modelled. The

capelin data obtained from the summer groundfish survey did not allow us to confirm or refute these results. An increase in the capelin biomass in the northern Gulf during the mid-1990s would not significantly change the modelling results. Indeed, if we increase the capelin biomass, production and consumption will increase accordingly through the production/biomass and consumption/biomass ratios. Capelin mainly consumed small and large zooplankton. Since the small and large zooplankton biomasses required to meet predator demands (marine mammals, fish, shrimp, and large crustacea here) were close to the lower production limits during the mid-1990s in the northern Gulf (Table 5), an increase in the capelin predation on zooplankton would have a weak impact on modelling results. Concerning the potential increase in capelin production, the single effect would be an increase in the other causes of mortality since predation and fishing mortality would not be affected by this change. However, even though trophic links involving capelin are relatively well estimated among ecosystems and periods (due to good local knowledge of diet compositions for all their predators, e.g., seals and cod), significant improvements in our understanding of the Gulf of St. Lawrence ecosystems would require local data pertaining to abundance and diet composition of this species.

The relative effects and interplay of fishing and predation on capelin have been poorly investigated in recent years. However, spatial and temporal variations in the capelin populations will inevitably influence landings and harvesting strategies. Many fisheries in the North Atlantic are managed by total allowable catches (TACs) and thus the exploitation rate or the biological reference points would have to be adjusted to the condition of the population (e.g., different conditions due to variations in mortality from predation and fishing, in reproductive parameters, age and length, fecundity, egg production). Total allowable catches for capelin reached about 7,500 metric tons in 2002 for the whole Gulf of St. Lawrence. Capelin stocks for the different management units are formally assessed every year and scientific information is taken into account in establishing fishery management plans. A comparison with a model developed for the recent period will identify and quantify the impact of different mortality processes on capelin and thus the effect of fishing and predation on capelin stock in the Gulf of St. Lawrence. The successful development of ecosystem models will provide powerful new tools for fishery management. The model solutions will be used as baselines (knowledge integration and expert systems) for the development of ecosystem-based management plans. The results already provide valuable information on the impact of fishing effort and capture rates of exploited species of these ecosystems and on the effects of the major mortality causes (fishing, predation, and natural mortality other than predation) on the fish and invertebrate communities.

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REFERENCES

Ajiad, A. M., and Pushaeva, T. 1991. The daily feeding dynamics in various length groups of the Barents Sea capelin during the feeding period. ICES Council Meeting Papers 1991/H16.

Allen, K. R. 1971. Relation between production and biomass. J. Fish. Res. Board Can. 28: 1573-1581.

Bowering, W. R., and Lilly, G. R. 1992. Greenland halibut (*Reinhardtius hippoglossoides*) off southern Labrador and northeastern Newfoundland (northwest Atlantic) feed primarily on capelin (*Mallotus villosus*). Neth. J. Sea Res. **29**: 211-222.

Bundy, A., Lilly, G. R., and Shelton, P. A. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 2310.

CAFSAC. 1994. Report on the status of groundfish stocks in the Canadian Northwest Atlantic. DFO Atl. Fish. Stock Status Rep. **94/4**.

Carscadden, J. E., and Frank, K. T. 2002. Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades. ICES J. Mar. Sci. **59**: 950-958.

Christensen, V., and Pauly, D. 1992. ECOPATH II - A system for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. **61**: 169-185.

DFO. 2001. Capelin of the Estuary and Gulf of St. Lawrence. DFO – Science, Stock Status Report B4-03.

DFO. 2003. Proceedings of the zonal assessment meeting – Atlantic cod. DFO Can. Sci. Advis. Sec. Proceed. Ser. 2003/021.

Froese, R., and Pauly, D. (Eds.). 2002. FishBase. World Wide Web electronic publication. [Online 25 September 2002] http://www.fishbase.org.

Gerasimova, O. V. 1994. Peculiarities of spring feeding by capelin (*Mallotus villosus*) on the Grand Bank in 1987-90. J. Northw. Atl. Fish. Sci. **17**: 59-67.

Gjøsæter, H., Dalpadado, P., and Hassel, A. 2002. Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance. ICES J. Mar. Sci. **59**: 959-967.

Grégoire, F., Lévesque, C., Poirier, G., and LeBlanc, C. 1999. Capelin (*Mallotus villosus*) catches and landings in the Estuary and Gulf of St. Lawrence for 1998. DFO Can. Stock Assess. Sec. Res. Doc. 99/09.

Harley, S. J., and Myers, R. A. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. Can. J. Fish. Aquat. Sci. **58**: 1569-1584.

Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**: 943-962.

Hutchings, J. A., and Myers, R. A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2216-2246.

Jangaard, P. M. 1974. The Capelin (*Mallotus villosus*). Biology, distribution, exploitation, utilization and composition. Bul. Fish. Res. Board Can. **186**, 70 pp.

Lawson, J. W., Anderson, J. T., Dalley, E. L., and Stenson, G. B. 1998. Selective foraging by harp seals, *Phoca groenlandica*, in nearshore and offshore waters of Newfoundland, 1993 and 1994. Mar. Ecol. Prog. Ser. **163**: 1-10.

Lilly, G. R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES Mar. Sci. Symp. **193**: 133-146.

Morissette, L., Despatie, S.-P., Savenkoff, C., Hammill, M. O., Bourdages, H., and Chabot, D. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). Can. Tech. Rep. Fish. Aquat. Sci. 2497.

MPO. 1999. Capelan de l'estuaire et du golfe du Saint-Laurent. MPO – Sciences, Rapport sur l'état des stocks B4-03.

Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1996. Hypotheses for the decline of cod in the North Atlantic. Mar. Ecol. Prog. Ser. **138**: 293-308.

NAFO (*Editors*). 1999. NAFO Statistical information. World Wide Web electronic publication. [On-line September 1999] http://www.nafo.ca.

O'Driscoll, R. L., Parsons, M. J. D., and Rose, G. A. 2001. Feeding of capelin (*Mallotus villosus*) in Newfoundland waters. Sarsia **86**: 165-176.

Panasenko, L. D. 1981. Diurnal rhythms and rations of capelin feeding in the Barents Sea. ICES Council Meeting Papers 1981/H 26.

Piatt, J. F., and Methven, D. A. 1992. Threshold foraging behaviour of baleen whales. Mar. Ecol. Prog. Ser. **84**: 205-210.

Pitt, T. K. 1973. Food of American plaice (*Hippoglossoides platessoides*) from the Grand Bank, Newfoundland. J. Fish. Res. Board Can. **30**: 1261-1273.

Savenkoff, C., Bourdages, H., Castonguay, M., Morissette, L., Chabot, D., and Hammill, M. O. 2004a. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (mid-1990s). Can. Tech. Rep. Fish. Aquat. Sci. 2531.

Savenkoff, C., Bourdages, H., Swain, D. P., Despatie, S.-P., Hanson, J. M., Méthot, R., Morissette, L., and Hammill, M. O. 2004b. Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s). Can. Tech. Rep. Fish. Aquat. Sci. 2529.

Savenkoff, C., Castonguay, M., Vézina, A. F., Despatie, S.-P., Chabot, D., Morissette, L., and Hammill, M. O. Inverse modelling of trophic flows through an entire ecosystem: the northern Gulf of St. Lawrence in the mid-1980s. Can. J. Fish. Aquat. Sci. (in press).

Vesin, J. P., Leggett, W. C., and Able, K. W. 1981. Feeding ecology of capelin (*Mallotus villosus*) in the Estuary and western Gulf of St. Lawrence and its multispecies implications. Can. J. Fish. Aquat. Sci. **38**: 257-267.

Vézina, A. F., and Pahlow, M. 2003. Reconstruction of ecosystem flows using inverse methods: how well do they work? J. Mar. Sys. **40-41**: 55-77.

Vézina, A. F., and Platt, T. 1988. Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Mar. Ecol. Prog. Ser. **42**: 269-287.

Whipple, S. J., Link, J. S., Garrison, L. P., and Fogarty, M. J. 2000. Models of predation and fishing mortality in aquatic ecosystems. Fish Fisheries **1**: 22-40.

Table 1. Functional groups used in modelling in the northern and southern Gulf of St. Lawrence for the two periods.

Group name	Main species
Cetaceans	*Balaenoptera physalus*, *B. acutorostrata*, *Megaptera novaeangliae*, *Phocoena phocoena*, *Lagenorhynchus acutus*, *L. albirostris*
Harp seals	*Phoca groenlandica*
Hooded seals	*Cystophora cristata*
Grey seals	*Halichoerus grypus*
Harbour seals	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *P. auritus*, *Larus delwarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)[a]	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)[a]	*Reinhardtius hippoglossoides*
Large American plaice (> 35 cm)[b]	*Hippoglossoides platessoides*
Small American plaice (≤ 35 cm)[b]	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleureonectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *Sebastes fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinnus*, *Centroscyllium fabricii*, *Anarhichas* spp., *Cyclopterus lumpus*, *Lycodes* spp., Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalus* spp., *Tautogolabrus adspersus*, *Macrozoarces americanus*, juvenile large demersals
Capelin	*Mallotus villosus*
Sand lance[c]	*Ammodytes* spp.
Arctic cod[d]	*Boreogadus saida*

Table 1. Cont.

Group name	Main species
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*
Piscivorous small pelagic feeders	*Scomber scombrus*, piscivorous myctophids and other mesopelagics, *Illex illecebrosus*, piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	*Clupea harengus harengus*, planktivorous myctophids and other mesopelagics, *Scomberesox saurus*, *Gonatus* spp., planktivorous juvenile large pelagics
Shrimp	*Pandalus borealis*, *P. montagui*, *Argis dentata*, *Eualus macilentus*, *E. gaimardi*
Large crustaceans	*Chionoecetes opilio*, other non-commercial species (e.g., *Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Stronglyocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Exogene hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)

Table 1. Cont.

Group name	Main species
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *C.* spp., *Leptocylindrus minimus*, *Thalassiiosira nordenskioldii*, *T.* spp., *Fragilariopsis* spp., and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, and Prymnesiophytes
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

[a]: Aggregated as Greenland halibut for the southern Gulf models.

[b]: Aggregated as American plaice for the northern Gulf models.

[c]: Included in the planktivorous small pelagic feeders for the southern Gulf models.

[d]: Included in the capelin group for the southern Gulf models.

Table 2. Observed biomass, lower and upper modelling constraints, and estimated fluxes for capelin made using inverse modelling for each ecosystem and each time period.

Parameter	Northern Gulf		Southern Gulf	
	Mid-1980s	Mid-1990s	Mid-1980s	Mid-1990s
Observed mean biomass (t km^{-2})	16.67	436.56[a]	0.49	21.53
Observed minimum biomass (t km^{-2})	0.07	173.67[a]	0.00	5.11
Observed maximum biomass (t km^{-2})	33.28	802.78[a]	0.98	48.81
Constrained minimum production (t km^{-2} yr^{-1})	0.04	0.08	0.001	2.31
Constrained maximum production (t km^{-2} yr^{-1})	19.99	481.70	0.61	29.29
Estimated production (t km^{-2} yr^{-1})	13.56	3.07	0.55	2.94
Biomass required to meet predator demands[b] (t km^{-2} yr^{-1})	10.84	2.71	0.52	2.15
Constrained minimum consumption (t km^{-2} yr^{-1})	0.56	0.27	0.49	21.53
Constrained maximum consumption (t km^{-2} yr^{-1})	264.22	100.38	26.88	1,344.99
Estimated consumption (t km^{-2} yr^{-1})	58.06	15.49	2.67	22.62
Constrained minimum catch (t km^{-2} yr^{-1})	0.01	0.00	0.000	0.001
Constrained maximum catch (t km^{-2} yr^{-1})	0.04	0.06	0.008	0.003
Estimated catch (t km^{-2} yr^{-1})	0.02	0.03	0.003	0.002

[a]: The observed biomass values for the 1994–1996 period seemed too high.
[b]: Predators were marine mammals and fish here.

Table 3. Diet compositions of capelin used in modelling of the northern Gulf for each time period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Northern Gulf					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Large Green. halibut						
Small Green. halibut						
American plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin	1.4	2.0	**0.0**	**2.8**	1.6	1.6
Sand lance	1.4	2.0	**0.0**	**2.8**	2.6	0.0
Arctic cod						
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp						
Large crustacea						
Echinoderms						
Molluscs						
Polychaetes						
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.1	0.0
Large zooplankton	46.5	17.9	**34.5**	**59.9**	36.5	48.7
Small zooplankton	50.7	19.8	**37.5**	**65.5**	59.2	49.7
Phytoplankton						
Detritus						
Total	100.0		72.0	131.0	100.0	100.0
TRN	5					

Table 4. Diet compositions of capelin used in modelling of the southern Gulf for each time period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. We used a coefficient of variation CV of 50% to calculate the upper and lower limits (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Southern Gulf (CV= 50%)					
Prey	Mean	± SD	Min	Max	Est. (mid-1980s)	Est. (mid-1990s)
Large cod						
Small cod						
Green. halibut						
Small Amer. plaice						
Large Amer. plaice						
Flounders						
Skates						
Redfish						
Large demersals						
Small demersals						
Capelin	**0.0**		0.0	0.0	0.0	0.0
Large pelagics						
Pisci. small pelagics						
Plank. small pelagics						
Shrimp						
Large crustacea						
Echinoderms						
Molluscs						
Polychaetes						
Other bent. inver.	**0.0**		0.0	0.0	0.0	0.0
Large zooplankton	6.3		**3.1**	**9.4**	6.7	6.0
Small zooplankton	93.7		**46.9**	**100.0**	93.3	94.0
Phytoplankton						
Detritus						
Total	100.0		50.0	109.4	100.0	100.0
TRN	4					

Table 5. Lower and upper production constraints and biomass required to meet predator demands for large and small zooplankton as estimated by inverse modelling for each ecosystem and each time period.

Parameter	Northern Gulf		Southern Gulf	
	Mid-1980s	Mid-1990s	Mid-1980s	Mid-1990s
Large zooplankton:				
Constrained minimum production (t km^{-2} yr^{-1})	15.43	14.00	15.43	12.00
Constrained maximum production (t km^{-2} yr^{-1})	38.57	35.00	38.57	40.00
Biomass required to meet predator demands[a] (t km^{-2} yr^{-1})	35.03	11.06	19.98	17.99
Small zooplankton:				
Constrained minimum production (t km^{-2} yr^{-1})	120.00	120.00	120.00	120.00
Constrained maximum production (t km^{-2} yr^{-1})	345.89	345.89	345.89	345.89
Biomass required to meet predator demands[a] (t km^{-2} yr^{-1})	55.43	10.72	19.73	38.28

[a]: Predators were marine mammals, fish, shrimp, and large crustacea here.

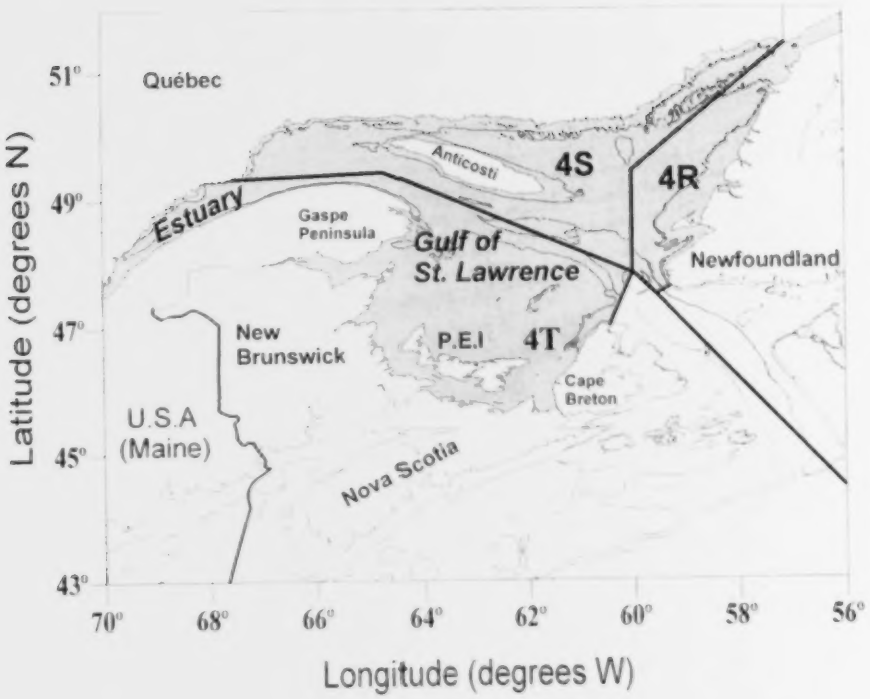


Figure 1. Study area: northern (NAFO divisions 4RS) and southern (NAFO division 4T) Gulf of St. Lawrence. The St. Lawrence Estuary was not included in this study.

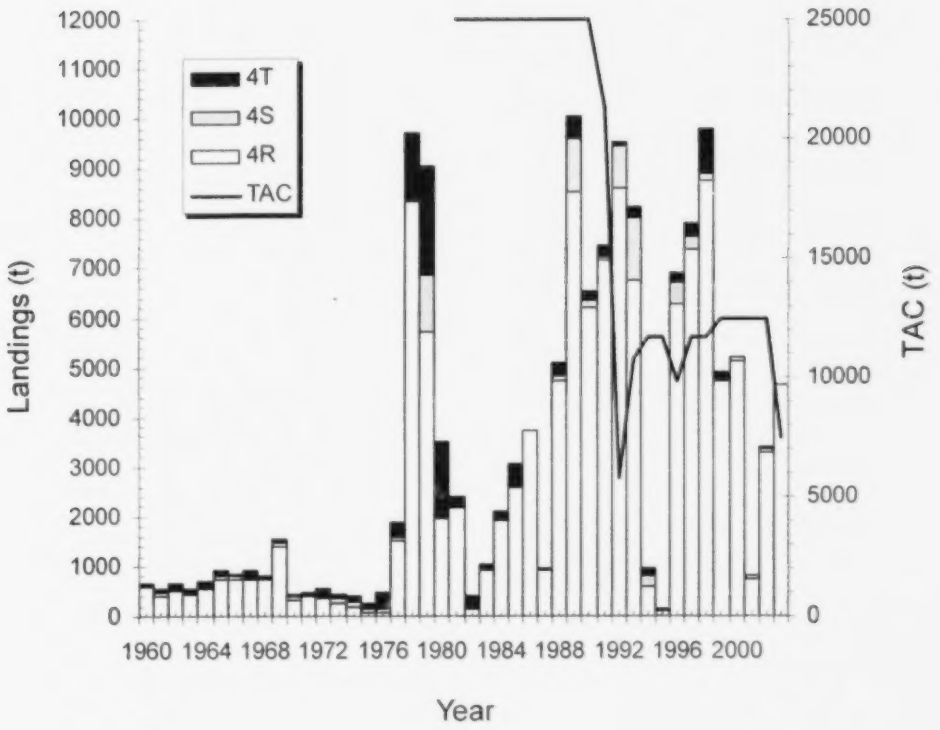


Figure 2. Total capelin landings and total allowable catch (TAC, t) for NAFO divisions 4RST since 1960.

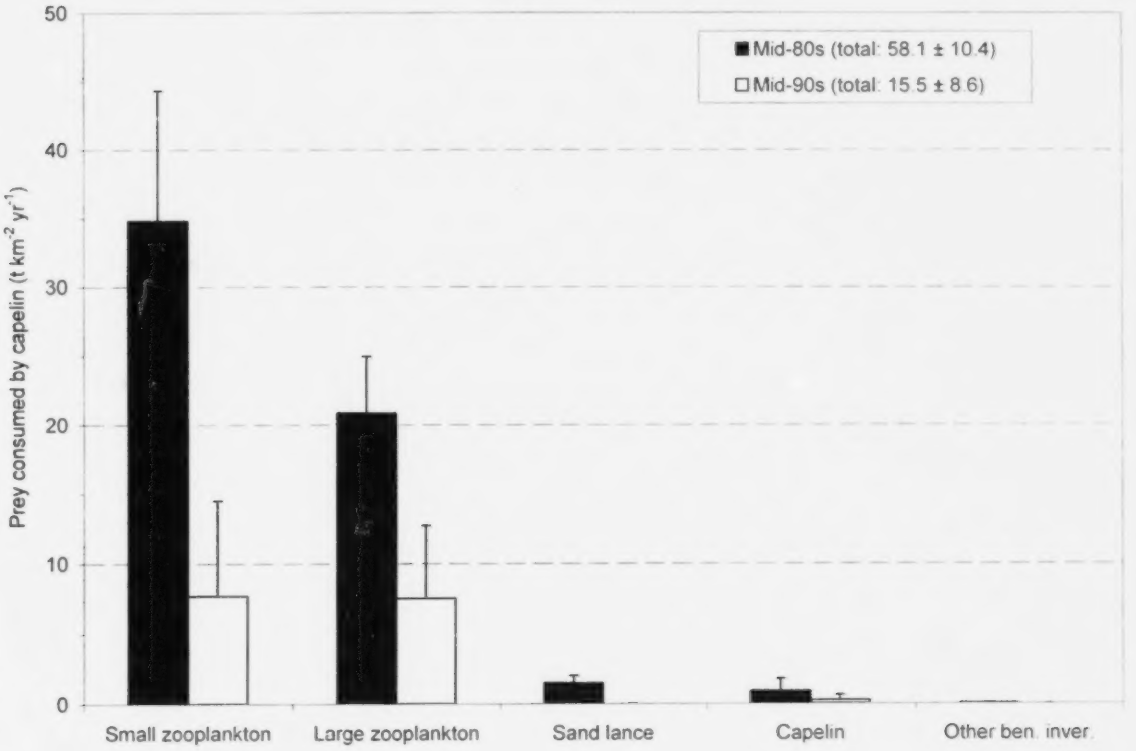


Figure 3. Main prey consumed by capelin estimated for each time period in the northern Gulf.

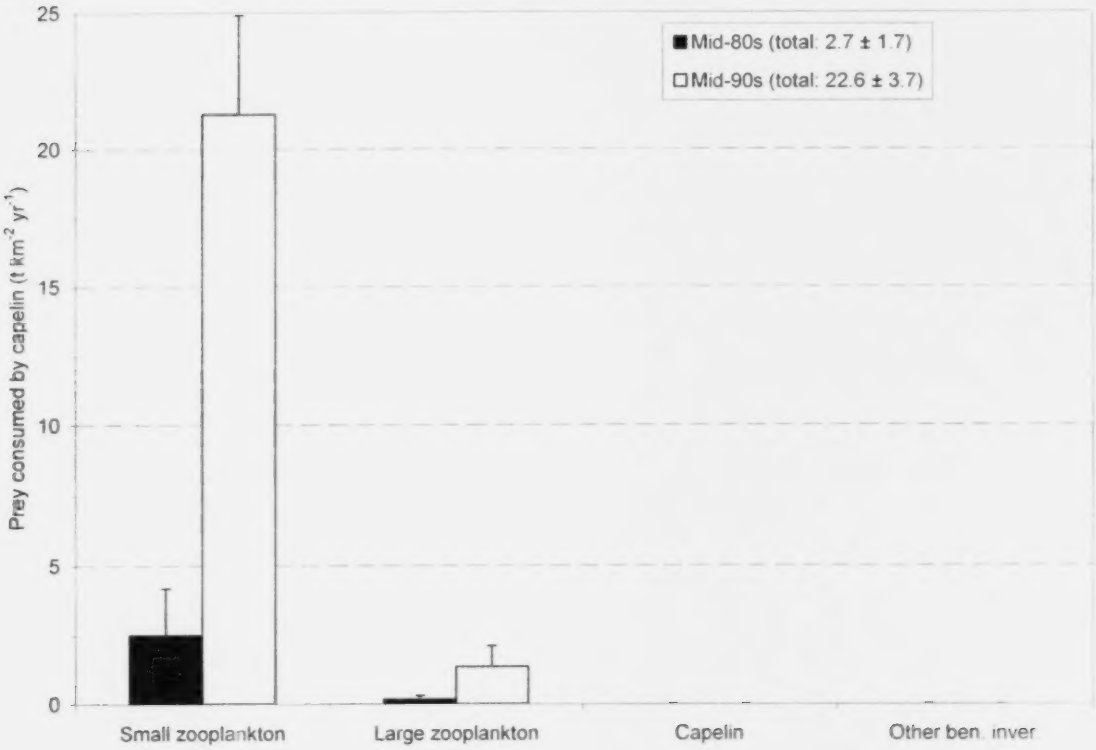


Figure 4. Main prey consumed by capelin estimated for each time period in the southern Gulf.

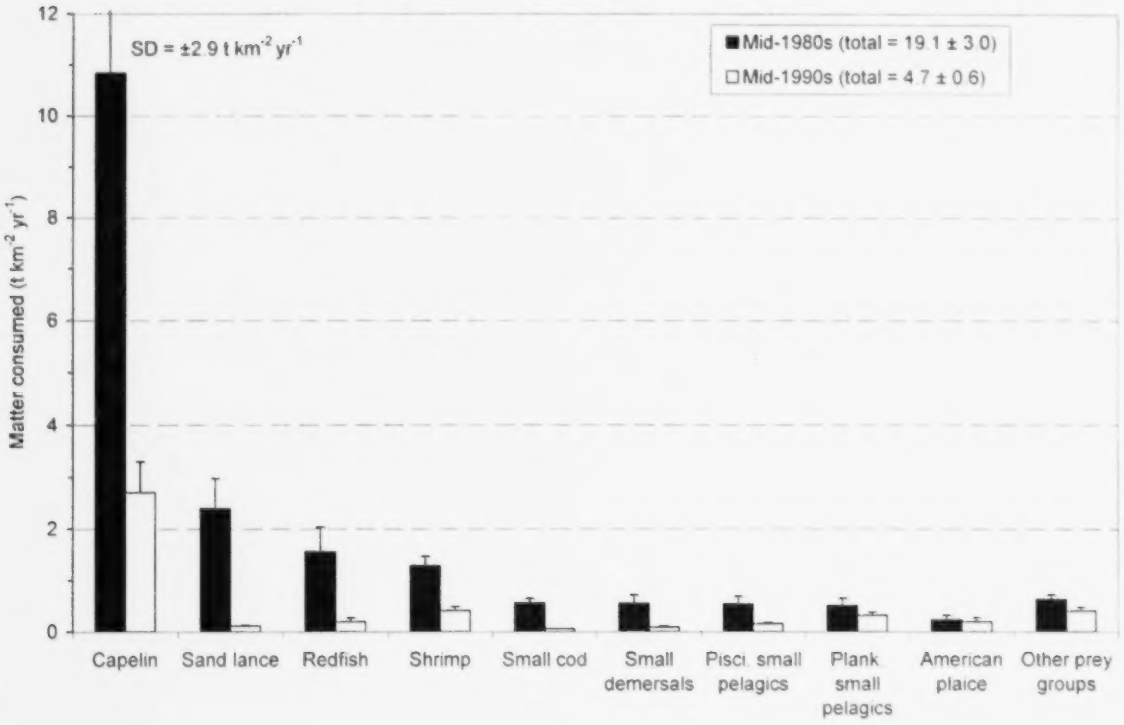


Figure 5. Main vertebrate, shrimp, and crustacean prey consumed in the northern Gulf estimated for each time period. SD is shown.

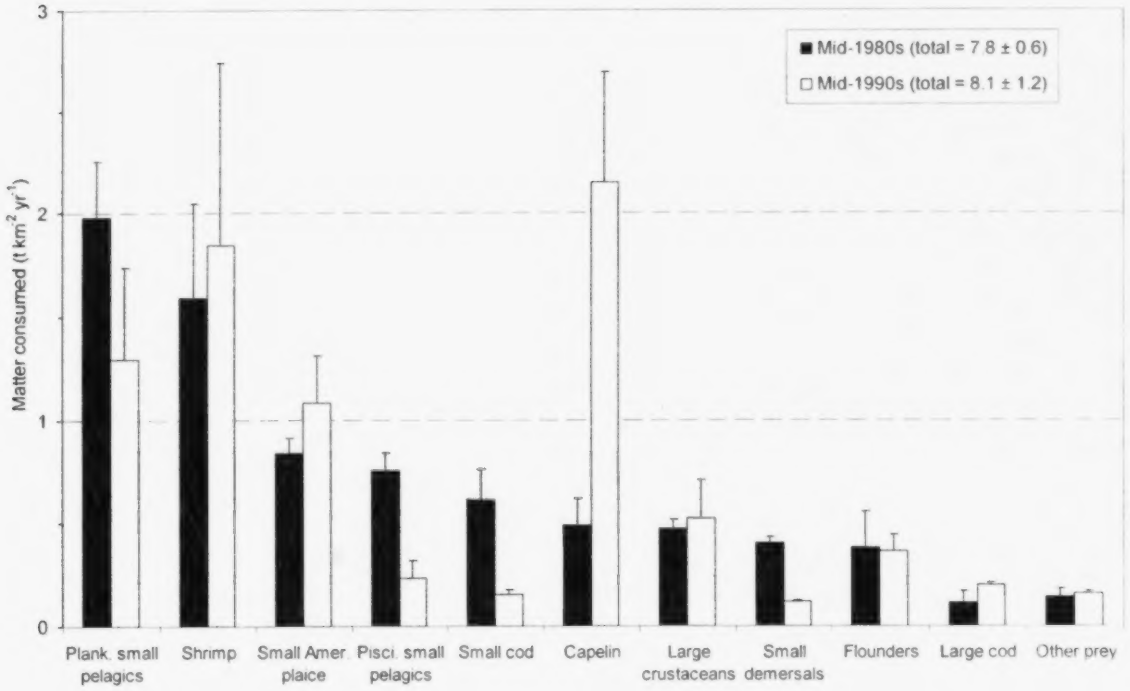


Figure 6. Main vertebrate, shrimp, and crustacean prey consumed in the southern Gulf estimated for each time period. SD is shown.

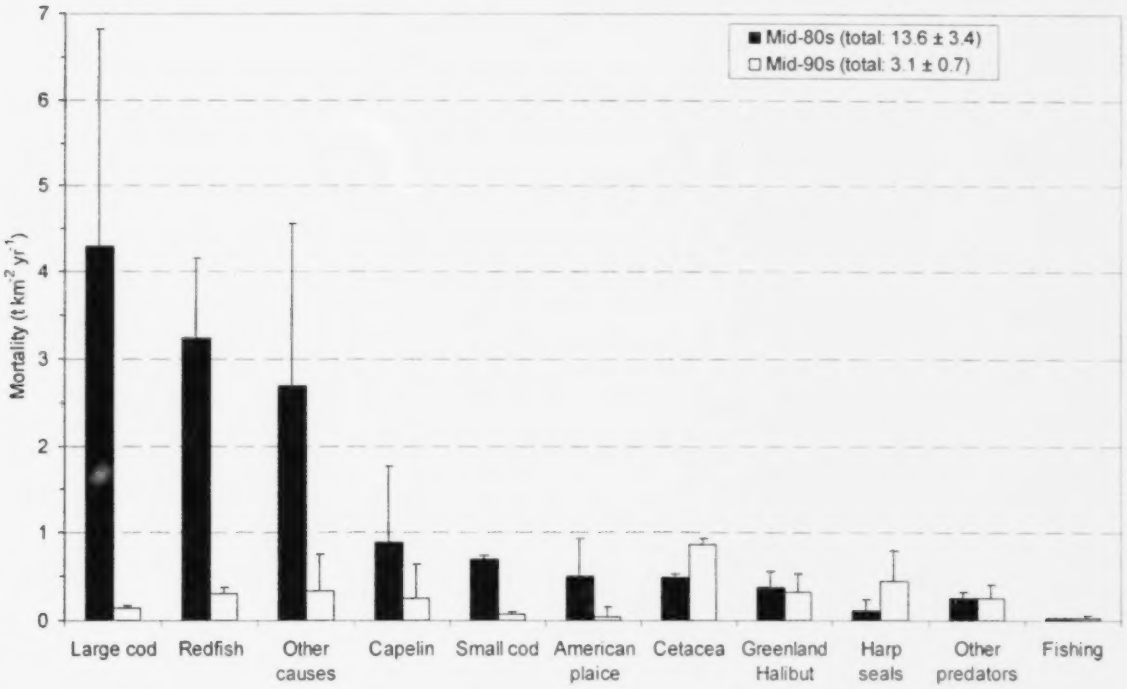


Figure 7. Main causes of capelin mortality (fishing, predation, and natural mortality other than predation, i.e., other causes) estimated for each time period in the northern Gulf.

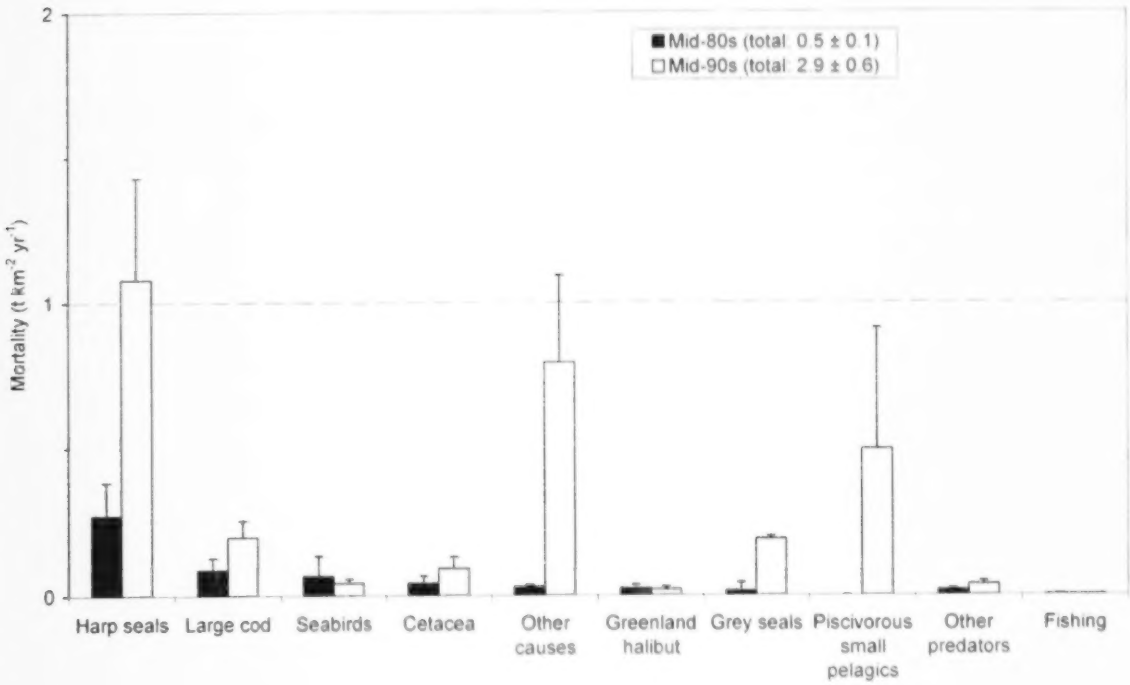
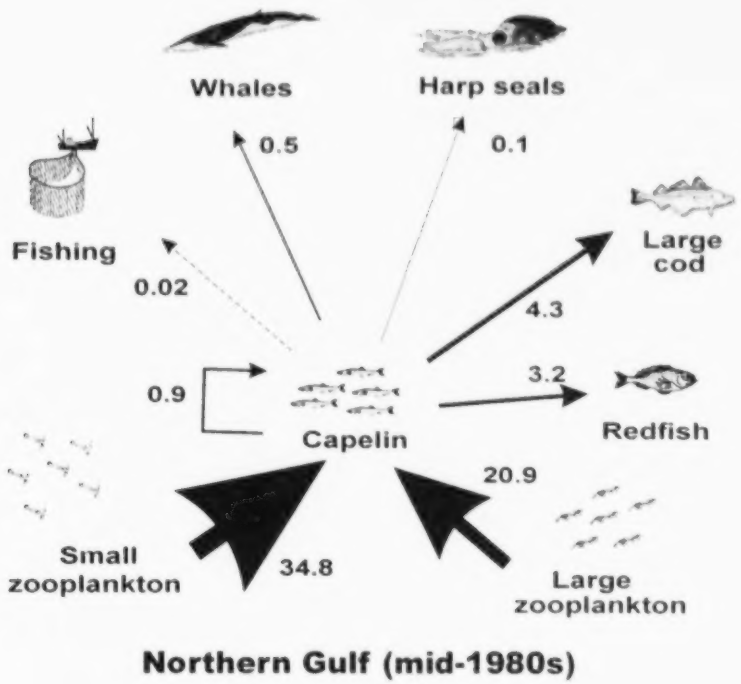
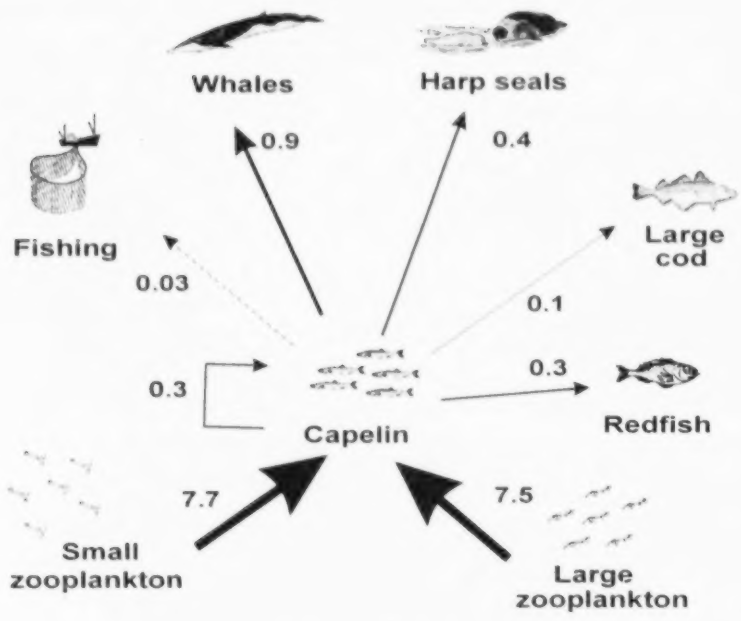


Figure 8. Main causes of capelin mortality (fishing, predation, and natural mortality other than predation, i.e., other causes) estimated for each time period in the southern Gulf.



Northern Gulf (mid-1980s)



Northern Gulf (mid-1990s)

Figure 9. Main trophic fluxes (t km^{-2} yr^{-1}) associated with capelin estimated for each time period in the northern Gulf. For comparison, fishing mortality fluxes (t km^{-2} yr^{-1}) are also included (dashed line).

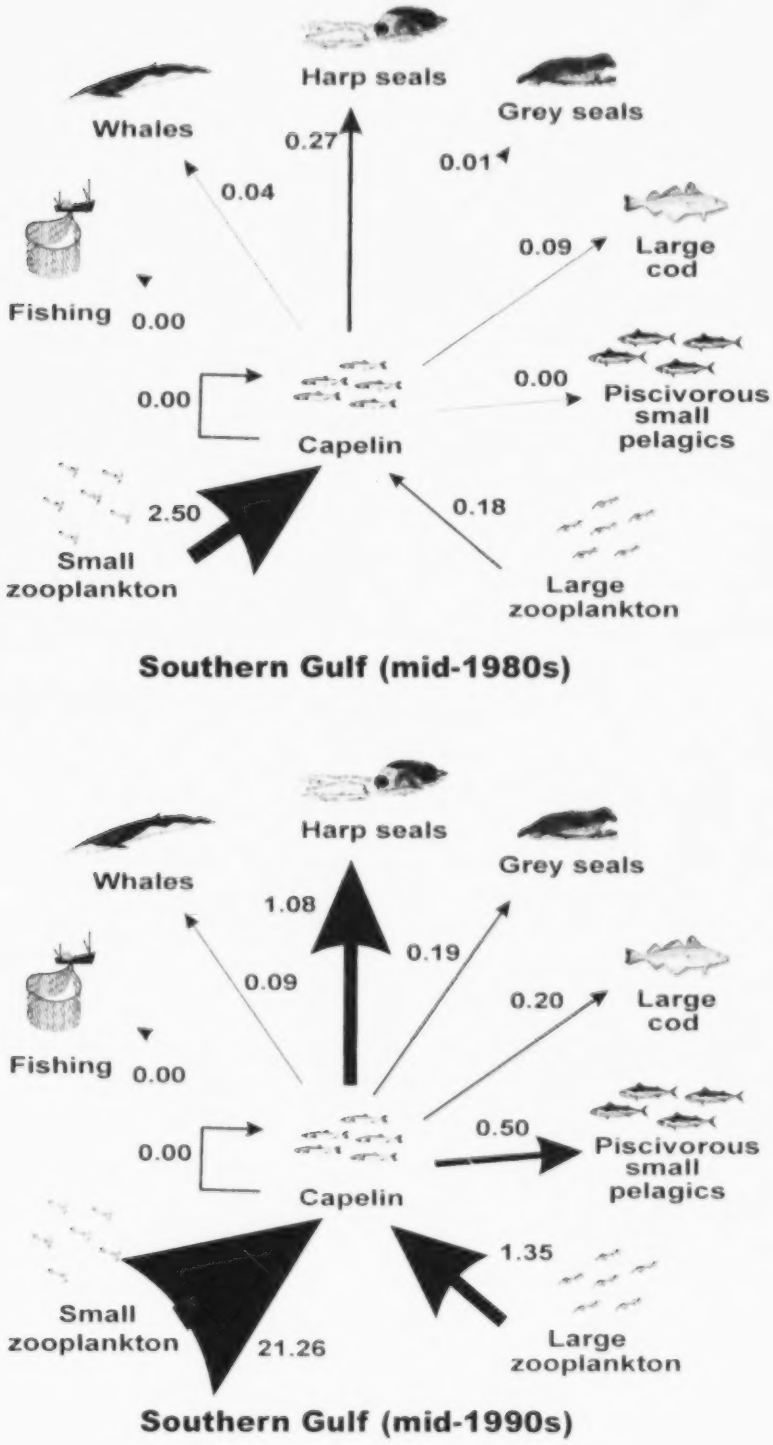


Figure 10. Main trophic fluxes (t km^{-2} yr^{-1}) associated with capelin estimated for each time period in the southern Gulf. For comparison, fishing mortality fluxes (t km^{-2} yr^{-1}) are also included (dashed line).